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REVISION OF BOUVARDIA (RUBIACEAE)¹

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ABSTRACT

The study of specimens, including many types, from 24 major North American and European herbaria has led to the recognition and description of 31 species of *Bouvardia*, including the novelty *B. standleyana*. The three subgenera proposed by Schlechtendal are retained as the foundation of taxonomic order in the genus, although their retention is admittedly partially fostered by convenience. Keys to the subgenera and species are presented and synonymy, typification and information on distribution and habitat are given for each species in so far as possible.

INTRODUCTION

Bouvardia, a rubiaceous genus of primarily small shrubs, is a notable but poorly understood component of the Mexican (with extensions into the south-western United States) and northern Central American flora. The habitat differs but is often a rocky outcrop of steep hillsides or barrancas at elevations above 500 meters, the ambient conditions varying from xeric to very mesic.

No economic significance is attributed to the genus. However, the attractive flowers of a number of species have led to their adoption as ornamentals, and artificial hybrids between some of them have been obtained. The nomenclature of these horticultural subjects is considered outside the scope of this study.

The taxonomy of *Bouvardia* has received little attention since Standley's treatment in the North American Flora (1921b), in which 30 species were recognized, a number being newly described. Since Standley's revision, descriptions of 19 additional species have appeared, scattered throughout the literature. The immediate needs in the genus were to evaluate the status of the species described since

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Standley's revision and re-evaluate those recognized by Standley. The recent aquisition of material by herbaria throughout the world has emphasized the pertinence of such a study.

The grouping of species within the genus has also been a matter of concern. Standley did not formally recognize the three subgenera introduced by Schlechtendal (1854), although his organization of species in the key corresponds closely to them. I have found Schlechtendal's subgenera to be at least a useful contrivance and consider their retention worthwhile for the sake of convenience alone. However, as nature is not systematically perfect, it is to be understood that some intermediacy exists between them, and that their delimitation is perhaps more pragmatic than phylogenetic.

The position of Bouvardia within the Rubiaceae has undergone drastic, and probably justified, alteration. Bouvardia, Heterophyllaea, Hindsia, Manettia, Danais, Coursiana and Hymenopogon were traditionally treated as members of the Cinchoneae (Hooker, 1873; Schumann, 1891). However, Bremekamp (1952) considered winged seeds (the only character uniting the tribe Cinchoneae) to be of little morphological significance and transfered these genera to the subfamily Rubioideae and tribe Hedyotideae (having transfered the tribe Hedyotideae from the subfamily Cinchonoideae) based on the presence of raphides, the absence of large pits in the basal wall of the testa cells, and the peltate placentas. Bremekamp reaffirms this transfer in a later paper (1966) in which he outlines his revisionary subdivision of the Rubiaceae.

Of the above genera, Bouvardia appears most closely related to Heterophyllaea and Hindsia from which it is distinguished by characters of the fruit and by flowers with four rather than five stamens and to Manettia from which it differs in its shrubby (not scandent) habit, terminal inflorescences and loculicidal capsules. It is doubtful that the position of placental attachment may be employed as a character delimiting Bouvardia and Mannetia, as attempted by Standley (1921a, see key). In specimens of both genera examined, the placenta is attached to the base of the septum. Bouvardia is distinguished from Hedyotis (sensu Lewis, 1961) by characters of the placenta, seed, endosperm and stipules.

Systematic Treatment³

Bouvardia Salisbury, Parad. Lond. pl. 88, 1807.

Aeginetia Cav., Anal. Ci. Nat. 3: 129, 1801; Ic. 6: 51, 1801, not Aeginetia L. (Sp. Pl. 632, 1753).

Shrubs, suffrutices or perennial herbs; raphides present. Leaves opposite or 3 to 4(-6)-nate, petiolate or infrequently sessile; stipules interpetiolar, consisting of a basal sheath and a usually trullate, green (not hyaline or scarious) mucro or free-portion; blades simple, entire, usually membranous. Inflorescences terminal, cymose (occasionally reduced to solitary flowers). Flowers actinomorphic, often showy; calyx-lobes 4, most often lanceolate, typically erect or ascending, persisting

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in fruit; corolla tubular or salverform, the tube usually well exceeding the lobes, the lobes 4 (very rarely 5 on the same plant), valvate; stamens 4, epipetalous, the anthers linear, dehiscing by longitudinal slits, usually included and subsessile in pin flowers (but typically positioned well above the middle of the corolla-tube), included or exserted (the filaments becoming free from the corolla-tube at the throat and extending beyond) in thrum flowers; ovary ± subglobose, inferior to 1/3 superior, the style single, slender (to ca l mm broad), compressed, elongate, exserted in pin flowers, included in thrum flowers, terminating in 2 rather short, linear, often minutely papillose style-branches. Capsules subglobose or slightly oblate, often somewhat compressed loculicidally, 2-celled (the septum complete), dehiscing loculicidally then septicidally, with a single ascending, fleshy, peltate placenta in each cell affixed to the based of the septum; seeds ∞, brown, vertically imbricate on the placenta, uniformly and ± evenly winged, the wing neither dissected nor fringed, the nucleus disciform, flattened or slightly pulvinate in crosssection, the testa cells thin-walled, lacking large pits in the basal wall, the endosperm fleshly.

Type: Bouvardia triphylla Salisbury [=B. ternifolia (Cav.) Schlecht.].

KEY TO THE SUBGENERA

a. Leaves opposite.
b. Inflorescences 3 to many-flowered, each partial inflorescence (flower or group of flowers, and their pedicels and peduncle, arising from each leaf-axil of the terminal 1-4 leaf-pairs of a floriferous stem tip) often composed of 3 or more flowers (sometimes of only 1); corolla tubular to salver-form, white or variously colored, the tube 0.4-3.5(-4.4) cm long, the lobes 1-7(-8.5) mm long, flared 10-90°; anthers in thrum flowers variously included or exserted. If the corolla is white (often greenish- or yellowish-white rather than pure white) and salverform and the partial inflores-

white rather than pure white) and salverform and the partial inflorescences are solitary flowers, then the floriferous branchlets are often very short and terminate in nodding, 3 to 7-flowered inflorescences (cf. B. multiflora)

I. Bouvardiastrum (p. 3)

bb. Flowers solitary or if the inflorescences several-flowered, then each partial inflorescence composed of only a solitary flower; corolla salverform, white, the tube (1.5-)3.5-8.5 cm long, the lobes (4-)7-28 mm long, flared at 90°; anthers included in thrum flowers or only the tips protruding

I. Subg. Bouvardiastrum Schlecht., Linnaea 26: 58, 1854.

Shrubs, suffrutices or rarely perennial herbs, the seasonal branches opposite, elongate or very short, pubescent or glabrous. Leaves opposite, typically petiolate; blades glabrous to conspicuously pubescent, the secondaries pinnate, less frequently subpalmate or plinerved, arcuate, rarely obscure, the reticulation obscure to prominent. Inflorescences few to many-flowered; partial inflorescences often composed of 3 or more flowers (occasionally 1-flowered). Flowers pedicellate or rarely sessile; calyx-lobes free to the floral cup or joined basally by a calyx-tube; corolla tubular to salverform, red, orange, yellow, violet, lavender, white, yellowish-white or greenish-white, externally glabrous or puberulent or more elongate-pubescent, the tube internally with a villous ring toward the base or more often generally

pilose or villous in the lower half, rarely entirely glabrous within; anthers included in pin flowers (rarely exserted), in thrum flowers included or often exserted; style glabrate or rarely pubescent, the branches 0.5-2.5(-4) mm long.

Lectotype: Bouvardia triflora H.B.K. [=B. multiflora (Cav.) Schultes & Schultes f.].

a. Leaf-blades typically pinnately nerved, less frequently subpalmately nerved (the majority of the secondaries arising ± together near the base of the midvein but at least 2 arising near the middle).

b. Corolla-tube with an internal villous ring toward the base.

cc. Stipular processes often filiform and terminally glandular; inflorescences 7 to 60-flowered; corolla externally glabrous, the lobes 2-4 mm broad

bb. Corolla-tube often pubescent in the lower half but the pubescence not organized into an isolated villous ring.

d. Calyx-lobes joined basally by a calyx-tube 0.5-2.5 mm long.

- e. Flowers short-pedicellate, not subtended by stipule-sheaths, the corolla externally minutely puberulent or glabrous.

dd. Calyx-lobes free to the floral cup.

- gg. Leaf-blades membranous, the secondaries readily evident their whole length; corolla variously colored.

h. Corolla externally puberulent or pubescent.

- i. Inflorescences obviously terminal on usually well-developed, leafy branches; corolla externally sparsely or densely pubescent with trichomes 0.3-1.3 mm long.
 - j. Seasonal branches distally glabrous or sparsely pilose; lower leaf-blade surface and distal portion of corollatube sparsely pilose; secondary veins subpalmate 8. B. subcordata
- ii. Inflorescences pseudoaxillary on greatly reduced, slender, leafless branchlets; corolla externally minutely papillose-puberulent (trichomes to 0.05 mm long) _______12. B. gracilipes

hh. Corolla externally glabrous.

- k. Seasonal branchlets distally glabrous or papillose-puberulent with trichomes to 0.2 mm long; leaf-blades with the secondary veins not brochidodrome, the reticulation obscure or inconspicuous; inflorescences with fewer than 15 flowers; corolla at least sparsely pilose in the lower half.
 - 1. Floriferous branchlets often suppressed (the vegetative portion as short as 2 mm); leaf-blades sparsely to

moderately papillose-puberulent above and below; floral cup minutely hirtellous with trichomes 0.05-0.3 mm long; calyx-lobes typically lanceolate, usually somewhat hirtellous; corolla white to greenish- or yellowish-white, less frequently yellow or red, tubular to salverform;

Il. Floriferous branchlets often well-developed; leaf-blades glabrate but often ciliate marginally; floral cup glabrous or obscurely puberulent with trichomes to 0.1 mm long; calyx-lobes linear or linear-lanceolate, often glabrate; corolla red or occasionally yellow, tubular; anthers included in thrum flowers or only the tips protruding

kk. Seasonal branchlets distally rather sparsely pilose to densely arachnose-pubescent with trichomes 0.2-1 mm long; leafblades with the secondary veins often brochidodrome, the reticulation prominent below; inflorescences usually more than 15-flowered; corolla entirely glabrous within

aa. Leaf-blades (3-)5-plinerved.

m. Inflorescences with fewer than 25 flowers; pedicels 6-13 mm long; calyxlobes deltoid-acuminate, ca l mm long; corolla-tube with an internal

mm. Inflorescences more than 25-flowered; pedicels 0.5-6 mm long; calyx-lobes lanceolate to linear or subulate, 2-9 mm long; corolla-tube often villous in the lower half but the pubescence not organized into a villous ring.

n. Reticulation of leaf-blades obscure above, inconspicuous below; calyxlobes lanceolate or elliptic-lanceolate, 1-2 mm broad; corolla tubular,

nn. Reticulation of leaf-blades visible above, prominent below; calyx-lobes linear-subulate, 0.3-1 mm broad; corolla tubular to salverform, violet or lavender, the tube 4.5-8.5 mm long; lower half of the style often

1. Bouvardia multiflora (Cav.) Schultes & Schultes f., Mant. Syst. Veg. 3: 118, 1827.

Aeginetia multiflora Cav., Anal. Ci. Nat. 3: 131, t. 28, fig. 2, 1801; Ic. 6: 52, t. 572, fig. 2, 1801.

Bouvardia versicolor Ker, Bot. Reg. 3: pl. 245, 1817. (Based on a greenhouse-grown plant, the illustration is taken as the type)

B. triflora H.B.K., Nov. Gen. Sp. Pl. 3: 386, 1820. (Type Humboldt & Bonpland s.n. P. not seen; fragment P)

B. cavanillesii DC., Prodr. 4: 366, 1830. (Based on Aeginetia multiflora)

Anotis longiflora Bentham, Pl. Hartw. 23, 1839. (Type Hartweg 206 GH, K; photo MICH) Bouvardia triflora var. hirsuta Martens & Galeotti, Bull. Acad. Bruxelles 11(1):236, 1844. (Type Galeotti 2658 BR)

B. bicolor Kunze, Linnaea 20: 24, 1847. (Based on garden plants grown from Mexican seed, the description is taken as the type)

B. mutabilis Walpers, Ann. Bot. Syst. Lipsiae 5: 127, 1849, as synonym of B. versicolor.

B. schiedeana Schlecht., Linnaea 26: 123, 1854. (Type Schiede s.n. B†)

Houstonia triflora (H.B.K.) A. Gray, Proc. Amer. Acad. Arts Sci. 4: 314, 1860. Bouvardia gracilis A. Gray, loc. cit. 22: 306, 1887. (Type probably Pringle 1255 G, GH)

B. versicolor var. graciliflora A. Gray in S. Watson, loc. cit. 416. (Syntypes Palmer 154, 369 & 708, all GH)

B. heterophylla Standley, N. Amer. Fl. 32: 107, 1921. (Holotype Heyde & Lux 3137 US 398167; isotype GH)

B. macrantha Standley, loc. cit. (Holotype Purpus 3981 US 841341; isotypes BM, F. GH. MO, UC)

B. latifolia Standley, loc. cit. 111. (Holotype Langlassé 246 US 385804; isotypes F fragment, GH, P)

B. salvadorensis Steyermark, Ceiba 4: 302, 1955. (Holotype Tucker 1368 F 1492726; isotypes MICH, UC, US)

Shrubs to 2 m; seasonal branchlets very short (2 mm) or to 10 cm or more in length, papillose-puberulent with trichomes to 0.2 mm long. Leaves with petioles to 5 mm long; blades most often ovate-lanceolate (varying from broadly ovate to narrowly lanceolate or elliptic-lanceolate), 0.7-6.7 cm long, 0.2-3.2 cm broad, membranous, sparsely or moderately hirtellous with papillose trichomes to 0.3 mm long, the secondaries 4-8, usually pinnate, the reticulation often obscure. Inflorescences terminal but often seemingly axillary by virtue of the very short branchlets, 3 to 7(-11)-flowered, often nodding; partial inflorescences 1 to 3-flowered; Flowers with pedicels 0.5-6(-16) mm long which are papillose-puberulent; floral cup hirtellous with papillose trichomes to 0.3 mm long; calyx-lobes typically lanceolate (varying from deltoid-acuminate to subulate), 1-8 mm long, usually somewhat hirtellous; corolla tubular to virtually salverform, white to greenish- or yellowish-white, less frequently yellow or red, glabrous, the tube 6-36(-44) mm long, internally sparsely pilosulous toward the base, the lobes 1-7(-8.5) mm long, spreading 10-90; anthers 1.5-2.5 mm long, in thrum flowers either exserted by 1-5 mm or included (tips sometimes protruding), included by 1-6 mm in pin flowers; style glabrous, the branches 1-4 mm long. Capsules 3-7 mm long, 3.5-9 mm broad; seeds 2-3.5 mm broad.

Holotype: MA, not seen. Cavanilles gives no information about the locality or collector in the original description.

Chihuahua to Nicaragua; no specimens known from Vera Cruz, Chiapas or the Yucatan Peninsula; moist slopes or ravines to dry, rocky hills or buffs; with pine-oak or thorn-scrub-cactus association; 1000-3000 m; flowering May through September.

Bouvardia versicolor, B. heterophylla, B. latifolia, B. macrantha and B. salva-dorensis are reduced to synonymy for the first time. I consider B. multiflora to be a polymorphic species, the description given encompassing the variability of specimens referred to all the above segregates.

The types of *B. heterophylla* (Guatemala) and of *B. salvadorensis* and certain collections from Temascaltepec, Mexico and Zitacuaro, Michoacan (*Hinton* 7899, 7911, 7925, 7933, 11996, all US) possess elongate pedicels (often 5-16 mm), short calyx-lobes (2 mm or less) and seasonal branches often more elongate than those of the average specimen of *B. multiflora*. Type specimens of *B. latifolia* and other Guerreran specimens such as *Crisman & Willis* 193 (MICH, TAES) and *Cooper & Rowell* 2511 (MICH) possess elongate (to 44 mm), subsalverform (lobes spreading at ca 60°), white corollas which closely approach the type of corolla found in the subg. *Bouvardioides*. The type of *B. macrantha* (Tlacuilotepec, Puebla) and collections from the vicinity of San Luis Tultitlanapa, Puebla (*Purpus* 3324, 3328, 3330, 3331, 3332, all MO) are characterized by rather elongate (to 36 mm), tubular corollas in which the anthers are included (or only the tips protruding) in thrum flowers. All these specimens are assignable to *B. multiflora* based on their total morphology and when all specimens of *B. multiflora* are considered, com-

plete intergradation is seen to exist. Attempting to formalize components of this reticulum of variation by the application of different Latin names would lead to confusion.

- 2. Bouvardia laevis Martens & Galeotti, Bull. Acad. Bruxelles 11(1):236, 1844.
- B. flava Decaisne, Fl. Serres 1: 215, pl. 38, 1845. (Based on a greenhouse-grown plant, the illustration is the type)

B. mollis Linden ex Schlecht., Linnaea 26: 85, 1854. (Type LZ†)

B. nubigena Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 382, 1940. (Holotype Steyermark 31901 F 1043221; photos F, TEX)

Shrubs to 1.5 m; seasonal branches usually well-developed, glabrous or distally sparsely papillose-puberulent with trichomes to 0.2 mm long. Leaves with petioles 1-7.5 mm long; blades ovate-lanceolate, subattenuate or subacuminate at the apex, 1.5-10.5 cm long, 0.7-5 cm broad, membranous, glabrate but often ciliate marginally with trichomes 0.05-0.8 mm long, less frequently sparsely puberulent above and below (often primarily along the veins), the secondaries 4-10, pinnate, the reticulation apparent or obscure. Inflorescences 3 to 11-flowered; partial inflorescences 1 to 5-flowered. Flowers with pedicels (1-)3-27 mm long which are glabrous to moderately papillose-puberulent; floral cup glabrous or sparsely puberulent with trichomes to 0.1 mm long; calyx-lobes linear-lanceolate or linear, glabrate or sparsely ciliate, 4-12 mm long; corolla tubular, red or occasionally yellow, glabrous externally, the tube 16-39 mm long, pilosulous in the lower half, the lobes 2.5-5.5 mm long, flared up to 40°; anthers 2-4 mm long, included or only the tips protruding; style glabrate, the branches 1-2.5 mm long. Capsules 4-9 mm long, 5-10 mm broad; seeds 2-3 mm broad.

Type: Mexico. Vera Cruz: ravines around Zacuapan, 3000 ft, April 1840, Galeotti 2600 (BR, F fragment ex G-Deless., P not seen; photo of P specimen at F, TEX, US).

Southwestern Tamaulipas to northwestern Oaxaca, Michoacan and southern Jalisco; centered in Hidalgo and western Vera Cruz; also found in Guatemala and extreme southern Chiapas; slopes of barrancas or rocky outcrops of mountain-sides; oak-pine woodlands in mesic to semi-arid conditions; 1000-3300 m; flowering April to August.

Bouvardia laevis and B. multiflora are closely related species and intermediates are sometimes encountered. Keying out a "problematical" specimen often requires consideration of a number of characters in combination (see key, p. 5), some of which are not statable in quantitative or absolute terms, and none of which will alone serve to identify the plant with certainty. Although it would be easy to build a case for combining these two species, the majority of specimens are easily identifiable and the extremes quite divergent. At present it seems unwise to combine them, increasing still further the complexity of the variation coming under the name B. multiflora.

- 3. Bouvardia Loeseneriana Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 11: 186, 1936.
- B. hintoni Bullock, Kew Bull. 1937: 307, 1937. (Type Hinton 8107 BM, F, G, GH, K, MO, US)

Shrubs, seasonal branches short or well-developed, glabrate. Leaves with petioles 2.5-11.5 mm long; blades ovate to ovate- or elliptic-lanceolate, basally cuneate to rounded, 2.5-9.8 cm long, 1.3-6.7 cm broad, sparsely pilosulous below and at the margins with white trichomes 0.2-1 mm long, glabrate above, the secondaries 4-12, pinnate, the reticulation apparent or obscure. Inflorescences (3-)7 to 20-flowered. Flowers with pedicels 0.5-5 mm lcng; floral cup glabrous to pruinose-puberulent (trichomes to 0.05 mm long) or hirtellous (trichomes to 0.5 mm long); calyx-lobes deltoid to broadly or narrowly lanceolate, 1-3(-4) mm long, marginally ciliate with trichomes to 0.2(-0.4) mm long, joined basally by a calyxtube 0.5-2 mm long; corolla typically salverform, white to greenish- or yellowishwhite, externally densely pruinose- or papillose-puberulent with white trichomes to 0.05 mm long or glabrous, the tube 24-32 mm long, internally sparsely or moderately pilosulous with trichomes 0.4-1 mm long, the lobes oblong-elliptic or oblong-lanceolate, 3.5-7 mm long, spreading at ca 90°, often arcuate; anthers 2-2.5 mm lcng, exserted in thrum flowers by 2-5 mm; style glabrate, the branches 0.5-2 mm long.

Holotype: Mexico. Guerrero: Texquitzín nr Chilapa, 28 Oct 1829, Schultes 89 (B†); isotype F (fragment).

Guerrero and the southern portion of the State of Mexico to Nayarit; precipitous mountainsides, wooded slopes and barrancas, steep ravines; typically in moist habitats but occasionally occurring in more arid barancas; 300-2400 m; flowering July through December.

In typical specimens of B. loeseneriana the corolla-tubes are minutely but densely pruinose- or papillose-puberulent externally, the floral cups glabrous or obscurely puberulent with trichomes to 0.05 mm long, the calyx-lobes deltoid or broadly lanceolate and not exceeding 3 mm, a calyx-tube to 2 mm long is present and the seasonal branches are well-developed (see types of B. loeseneriana and B. hintoni and such collections as Hinton 10521, US; 15003, US; 15979, US; McVaugh & Koelz 1046, MICH). However, in Colima, southwestern Jalisco and Nayarit, variable specimens are encountered with glabrous corolla-tubes, glabrous or pruinose-puberulent (trichomes to 0.05 mm long) or conspicuously hirtellous (trichomes to 0.5 mm long) floral cups, often slender-lanceolate calyx-lobes to 4 mm long and short or elongate seasonal branchlets (see McVaugh 15260, 18060, 18964, 19832; Wilbur & Wilbur 2335, 2439, 2440, 2464, 2465; all MICH). Specimens with glabrous corollas, hirtellous floral cups, slender-lanceolate calyx-lobes and short branchlets are difficult to distinguish from B. multiflora and are doubtless closely allied to the latter. They differ from B. multiflora in the presence of a calyx-tube and usually in the more numerous flowers (more than 7) of the inflorescence.

4. Bouvardia capitata Bullock, Hook. Ic. Pl. t. 3296, 1935.

Shrubs to 1.5 m; seasonal branchlets rather elongate, to 2 mm broad, woody or suffrutescent, glabrous or sparsely pilose distally with trichomes to 0.7 mm long. Leaves with petioles 1-14 mm long; blades ovate to suborbicular or broadly elliptic, 2-10.3 cm long, 1.3-6.3 cm broad, usually sparsely pilose with white trichomes

to 1 mm long (occasionally restricted to the margins), the secondaries 4-10, pinnate or the lower 4-6 arising subpalmately near the base of the midvein, the reticulation obscure. Inflorescences capitate, 6 to 36-flowered. Flowers sessile, each subtended by the stipule-sheath of a bract-pair; floral cup typically glabrous; calyxlobes linear-lanceolate, 3-8 mm long, pilosulous toward the margins with trichomes 0.3-0.8 mm long, joined basally by a calyx-tube 1-2.5 mm long; corolla \pm salver-form, probably white, glabrous externally, the tube 15-23 mm long, pilosulous in the lower half; the lobes 3-7 mm long, oblong, spreading to 90°, often arcuate; anthers 1-2 mm long, exserted by 2-4 mm in thrum flowers; style glabrous. Capsules 4.5-8 mm long, 4.5-11 mm broad; seeds 2.5-4 mm broad.

Type: Mexico. Mexico: Distr Temascaltepec, Palmar, in a barranca, 7 July 1934, Hinton 6319 (BM, F, K).

Known only from the District of Temascaltepec in the State of Mexico; barrancas and open woodlands at 1000-1500 m; flowering in July and August.

As pointed out by Bullock (loc. cit.) the congested inflorescence of *B. capitata* is distinctive, probably representing a reduction from a compound dichasium. The base of each sessile flower is surrounded by the often membranous and pluriaristate stipule-sheath of a bract-pair, the lamina being suppressed. The flowers are grouped in threes and then in multiples of three, each flower-group or partial inflorescence being in turn subtended by a stipule-sheath showing an increasing development of the bract lamina.

Bouvardia capitata is closely related to B. loeseneriana, but in addition to the sessile flowers subtended by stipule-sheaths, specimens of B. capitata may often be distinguished by the glabrous corollas with the tube usually less than 23 mm long, linear-lanceolate calyx-lobes typically exceeding 3 mm in length and possessing a more elongate marginal pubescence, and the always glabrous floral cups.

- 5. Bouvardia cordifolia DC., Prodr. 4: 366, 1830.
- ? Hedyotis lutea Sessé & Mociño, Fl. Mex. 22, 1891. (Type Sessé & Mociño s.n. MA, not seen).

Shrubs, slender or suffrutices to 1 m; seasonal branches ascending, distally sparsely to densely papillose-puberulent or villosulous with white trichomes 0.05-1 mm long. Leaves with pubescent petioles 0.5-2(-7) mm long; blades broadly ovate to ovate-lanceolate, cordate or rounded at the base, 1.5-6.6 cm long, 0.7-5.2 cm broad, sparsely puberulent with papillose to villous trichomes 0.05-1 mm long, the secondaries 4-12, pinnate, the reticulation often conspicuous below. Inflorescences 7 to 50-flowered, subcapitate. Flowers with pedicels 0.5-2.5(-8) mm long which are sparsely to densely pubescent; floral cup glabrate to densely white-pubescent with trichomes 0.05-0.8 mm long; calyx-lobes lanceolate to subulate, 1.5-7.5 mm long, joined basally by a calyx-tube 0.5-2 mm long; corolla tubular, red-orange or apricot (the lobes and extreme distal part of the tube yellow) minutely white-papillose-puberulent externally with trichomes to 0.05 mm long, less frequently glabrous, the tube 12-30 mm long, pilose in the lower half but lacking a villous ring, the lobes ovate or deltoid to oblong or elliptic-lanceolate, flaring up to 45°, 1.2-5 mm long; anthers ca 2 mm long, brown, included by 1-6 mm

or the tips protruding; style papillose-puberulent to glabrate, white, the branches 1-1.5 mm long. Capsules 3.5-6 mm long, 4-7 mm broad; seeds 1.5-3.5 mm broad.

Type: Mexico: Sessé & Mociño s.n. (MA, not seen); pl. 487 of the Calques des dessins . . . is a drawing of the type.

Mexico, Michoacan, Oaxaca, Guerrero, Colima and Jalisco; steep moist slopes, shady arroyas or dry rocky cliffs or barrancas; often in oak or pine-oak woodlands; 200-2850 m; flowering June through November.

The majority of specimens of *B. cordifolia* deposited in herbaria are from the vicinity of Morelia, Michoacan and Temascaltepec, Mexico and are characterized by the minute but often dense external puberulence of their corollas (see *Blackwell 26 & 27*, TEX; *Hinton 7950*, F; *Hitchcock & Stanford 7146*, US; *Kenoyer A263*, F; *Rzedowski 20775*, ENCB). A few scattered collections of *B. cordifolia* have been made in Colima, southern Jalisco, Guerrero and Oaxaca, but these are all distinguished by glabrous corollas (see *Iltis et al. 570*, *McVaugh 15010 & 15813*, *Ryan & Floyed 37*, all MICH). As I have found no other character correlated with the difference in pubescence of the corolla which might serve to delimit these two "groups" of *B. cordifolia*, and since their apparent geographic separation may result from insufficient collecting rather than natural disjunction, I have not recognized them by formal infraspecific categories. It is perhaps worth mentioning that an analogous situation involving pubescent and glabrous forms exists in *B. loeseneriana* and that the geographic area of interest and pattern of distribution are roughly similar.

6. Bouvardia conzattii Greenman, Proc. Amer. Acad. Arts Sci. 39: 92, 1903.

Shrubs; seasonal branchlets often distally white-papillose-puberulent with trichomes 0.05-0.1 mm long. Leaves with petioles 1-3 mm long; stipular processes lanceolate; blades ovate to lanceolate, 1.5-5 cm long, 0.4-2.8 cm broad, basally cuneate to broadly rounded, minutely papillose-hispidulous marginally and often sparsely so above and below (primarily along the main veins below) with trichomes 0.05-0.25 mm long, the secondaries 6-10, pinnate or occasionally the lower 4-6 arising subpalmately near the base of the midvein, the reticulation usually obscure. Inflorescences 7 to 12-flowered. Flowers with pedicels 0.5-5.5 mm long; floral cup glabrate; calyx-lobes linear or linear-lanceolate, 2.5-5.5 mm long, 0.3-0.8 mm broad, free to the floral cup; corolla tubular, red or yellowish-red, very minutely papillose-puberulent externally with trichomes less than 0.05 mm long (sometimes only sparsely so), the tube 8-17 mm long, 1.5-2 mm broad at the neck, internally with a villous ring toward the base, the lobes ovate to deltoid, 1-2 mm long, to 1.3 mm broad; anthers 2-3 mm long, included by 1-4.5 mm; style glabrate. Capsules 2.5-4.5 mm long, 3-5.5 mm broad; seeds 1.3-2 mm broad.

Holotype: Mexico. Oaxaca: 1750 m, July-Aug 1901, Conzatti & Gonzáles 1067 (GH). (sphalm. Conzatti & Gonzáles 1076 by Greenman)

Known only from Oaxaca; 1600-2000 m; known to be in flower May through August.

7. Bouvardia chrysantha Martius, Del. Hort. Monac. Sem. 1848: 4, 1848 (not seen); Ann. Sci. Nat., Bot., sér. 3, 11: 247, 1849.

B. myrtifolia Schlecht., Linnaea 26: 121, 1854. (Type Schiede s.n. B†)

B. macilenta Blake, Contr. Gray, Herb. 53: 65, 1918. (Holotype Conzatti & Reko 3288 GH)

B. cataphyllaris Bullock, Hook. Ic. Pl. t. 3297, 1935. (Type Hinton 1131 BM, F, G, GH, K, MICH, MO, US)

Shrubs or suffrutices to 1 m; seasonal branchlets well-developed or very short, glabrous or distally papillose-puberulent (trichomes to 0.1 mm long) or pilosulous (trichomes to 1 mm). Leaves with petioles 0.5-3 mm long; blades ovate to elliptic or lanceolate, 1-7.8 cm long, 0.4-3 cm broad, often somewhat conduplicate, slightly crassulate, pale-satiny-green below, glabrous or sparsely puberulent with white trichomes 0.1-1 mm long (sometimes limited to the margins and midvein), rarely more densely pubescent, the secondaries usually totally or partially obscure, the reticulation not visible. Inflorescences 5 to 25-flowered, usually subcapitate. Flowers with pedicels 0.5-4 mm long; floral cup green, glabrous or occasionally pubescent; calyx-lobes linear-lanceolate to slender-subulate, 2.5-11 mm long, free to the floral cup; corolla tubular, red-orange (the lobes and extreme distal part of the tube yellow), externally glabrous or rarely sparsely pilosulous with white trichomes to 1 mm long, the tube 15-34 mm long, 2-4 mm broad at the neck, sparsely pilosulous in the lower half (trichomes ca 0.5 mm long), the lobes ovate to oblong, 1.5-4 mm long, 1-3 mm broad, flared up to 40°; anthers white or yellow-white, 1.5-3 mm long, included by 1-6 mm or the tips protruding; style glabrate, white or yellowwhite. Capsules 3.5-8.5 mm long, 4.5-10 mm broad; seeds 2.5-3.5 mm broad.

Type: "Mexico": nr Sanjaguillo, Karwinsky s.n., not seen.

Oaxaca and extreme southern Peubla to Jalisco; dark loamy soil of volcanic slopes or rocky bluffs of barrancas; oak zone; 1300-2900 m; flowering mostly from June through October.

Except for the small size of all structures, the type specimen of B. macilenta falls within the limits of variation under the name B. chrysantha.

Certain specimens of B. chrysantha such as Hinton 10471 (MO, US) & 10541 (MO, US) and the type of B. cataphyllaris resemble B. multiflora in their short floriferous branchlets, hirtellous floral cups and often partially evident secondary veins. It is thus probable that B. chrysantha intergrades to a limited extent with B. multiflora. However, B. chrysantha is retained as a separate species since all but a few specimens are clearly distinct from B. multiflora. As already indicated, combining closely related species with B. multiflora would only lead to the creation of one hopelessly polymorphic species.

8. Bouvardia subcordata Standley, N. Amer. Fl. 32: 105, 1921.

Shrubs, the seasonal branches glabrous or pilose distally and at the nodes. Leaves with petioles 1-5 mm long; blades ovate to suborbicular, basally broadly rounded or cordate, 1.8-4.3 cm long, 1.2-3.4 cm broad, membranous, moderately or rather sparsely (but evenly) pilose with white trichomes 0.2-1 mm long, the secondaries 6-8, the lower 4-6 often arising subpalmately near the base of the midvein, the reticulation obscure. Inflorescences 3 to 7-flowered. Flowers with pedicels 1-5 mm long which are puberulent with white trichomes ca 0.5 mm long; floral cup tomentose; calyx-lobes lanceolate or elliptic-lanceolate, 2-7.5 mm long, sparsely pilose, free to the floral cup; corolla tubular, red (?), externally rather sparsely

white-pilose distally with trichomes 0.3-1 mm long, the tube 15-31 mm long, 2.5-4.5 mm broad at the neck, pilose in the lower half, the lobes ovate to ovate-orbicular or rhombic, 2-4 mm long; anthers 2-2.5 mm long, included or the tips protruding; style glabrate.

Holotype: Mexico. Sinaloa: betw Rosario & Colomas, 13 July 1897, Rose 1628

(US 300476); isotype F.

Known only from the type collection.

9. Bouvardia xylosteoides Hooker & Arnott, Bot. Beechey Voy. 428, 1840.

B. villosa Standley, N. Amer. Fl. 32: 107, 1921. (Holotype Conzatti 1486 US 764094; isotype GH)

Shrubs, the seasonal branchlets densely white-villous at least distally with trichomes to 1 mm long. Leaves with villous petioles 1-6 mm long; blades ovate to elliptic, basally cuneate to rounded, 1.3-3.3 cm long, 0.8-2 cm broad, villous with trichomes to 1 mm long (densely villous-tomentose below), the secondaries 4-8, pinnate, the reticulation obscure. Inflorescences 3 to 7-flowered. Flowers with villosulous pedicels 0.5-2 mm long; floral cup tomentose; calyx-lobes lanceolate or linear-lanceolate, 2-8 mm long, rather densely pubescent; corolla tubular, densely white-villous on the upper two-thirds with trichomes 0.4-1.3 mm long (sparsely pubescent toward the base), the tube 13-26 mm long, sparsely pilose within near the base, the lobes ovate, 1.5-3.5 mm long; anthers 2-4 mm long; style glabrous.

Type: Mexico. Oaxaca: low mountains around Mitla (sphalm. Mitlam by Hooker & Arnott), Andrieux 333 (F fragment ex G-Deless., G, K).

Bouvardia xylosteoides has been collected at 1800 m and is known to be in flower from May through July; all collections known (three, including the type collection) are from central Oaxaca.

- 10. Bouvardia dictoneura Standley, N. Amer. Fl. 32: 109, 1921.
- B. matudai Lundell, Lloydia 2: 105, 1939. (Holotype Matuda 2667 MICH; isotypes F, MO, US; photos F, TEX)
- B. venosissima Lundell, Bull. Torrey Bot. Club 66: 602, 1939. (Holotype Matuda 2748 MICH)
- B. pachecoana Standley & Steyermark, Publ. Field Mus. Nat. Hist., Bot. Ser. 23: 22, 1943. (Holotype Standley 86226 F 1093896; isotypes A, US; photo US)

Shrubs, slender, to 2.5 m; seasonal branches often elongate, slender, suffrutescent, bisulcate, sometimes sparsely pilose along the margins of the sulcae with trichomes 0.1-0.8 mm long, otherwise glabrous. Leaves with petioles 0.5-10 mm long; stipular processes 1.5-10.5 mm long, often filiform, glandular at the tip; blades ovate to lanceolate, basally rounded or cordate, 2-10.6 cm long, 1-5.8 cm broad, usually glabrous but often ciliate marginally with trichomes 0.1-1 mm long, occasionally sparsely pilose above and below with trichomes to 1 mm, the secondaries 4-12, pinnate or rarely subpalmate, the reticulation obscure to prominent. Inflorescences 7 to 60-flowered. Flowers with pedicels (1-)3-10 mm long; floral cup glabrous; calyx-lobes linear-lanceolate or linear-subulate, 1.5-6 mm long; corolla red or orange-red, externally glabrous, the tube 4-13.5(-20) mm long, 2-4.5 mm broad at the neck, a villous ring within toward the base, the lobes broadly ovate or rhombic to somewhat oblong, 1.5-6 mm long, 2-4 mm broad, flared up to

60°; anthers 2-3 mm long, included by 1-7 mm or the tips protruding; style glabrate. Capsules 3-5 mm long, 3.5-6 mm broad; seeds 1-2 mm broad.

Holotype: Mexico. Chiapas: Chicharras (sphalm. Chichorras by Standley), 3000-6000 ft, 6 Febr 1896, Nelson 3757 (US 256554); isotype GH.

Southwestern Guatemala and southern Chiapas; volcanic slopes, often in pine forests; 1000-3800 m; apparently flowering the year round.

A collection from Guerrero (Pilas-Pasion, Distr Montes de Oca), Hinton 10759 (UC, W), has 3-nate leaves (a characteristic of the subg. Bouvardia) but is otherwise indistinguishable from many specimens of B. dictyoneura. Field work is needed in the attempt to find additional specimens with ternate leaves and to assess the reality of the apparent geographic separation from typical opposite-leaved forms.

11. Bouvardia standleyana Blackwell, sp. nov.

Frutex B. gracilipedi affinis, sed foliorum laminis supra saltem sparse pubescentibus, inflorescentiis terminalibus in ramis foliosis elongatis dispositis, corollaque omnino glabro differt.

Shrubs; seasonal branches 7-30 cm long, suffrutescent, distally sparsely pilose (often irregularly so) to densely arachnose-pubescent with white trichomes 0.2-1 mm long. Leaves with petioles 1-7.5 mm long; blades ovate to trullate, 1.5-7.5 cm long, 0.8-4.3 cm broad, membranous, at least sparsely pubescent on both surfaces with white trichomes 0.2-1 mm long (below primarily concentrated along the main veins, the trichomes often spreading or curling), occasionally densely arachnose-puberulent below, the secondaries 6-12, pinnate, often brochidodrome, the reticulation apparent above, prominent below. Inflorescences (10-)15 to 50-flowered, terminal on leafy branches more than 7 cm long (including flowers) and more than 1 mm broad. Flowers with pedicels 3-14 mm long (at least a few pedicels 8 mm or more) and less than 0.5 mm broad; floral cup sparsely pilosulous to conspicuously hirsute with trichomes 0.2-0.7 mm long or glabrous; calyx-lobes lanceolate or elliptic-lanceolate to subulate, 1-3 mm long; corolla tubular, yellow or light orange, externally and internally glabrous, the tube 7-24 mm long, the lobes ovate or deltoid to oblong, 2-4 mm long, flared up to 45°; anthers 1-2 mm long, exserted by 1-3.5 mm in thrum flowers, included by 1-2 mm in pin flowers; ovary subglobose, ca 1 mm long, the style glabrous, with branches 1-2.5 mm long.

Holotype: Mexico. Michoacan: Distr Coalcoman, S of Naranjillo, 1360 m, 26 Nov 1938, *Hinton 12677* (US 2020693); isotypes K, MICH, UC.

Western Jalisco, Michoacan and Guerrero; mountain summits, steep mountainsides or rocky slopes; often found in the oak zone but occasionally in sandy soil in association with more tropical vegetation; 800-1700 m; flowering September through February.

Bouvardia standleyana is distinguished from its nearest relative, B. gracilipes, by the glabrous corollas (externally and internally), the well-developed and leafy floriferous branches, the presence of pubescence on the upper blade surface (though often sparse) and the more elongate pubescence on the distal portion of the seasonal branches.

Two collections, *Hinton 14901* (US) & 15408 (F), from Mina, Guerrero are interesting in their apparent intermediacy between *B. standleyana* and *B. bouvardioides* (subg. *Bouvardia*). Although the majority of floral and inflorescence characters, as well as the pilose to arachnose pubescence of the branchlets and leaves resemble *B. standleyana*, the leaf size, form, verticillation and the red corollas strongly suggest specimens of *B. bouvardioides* from the Western Sierra of Mexico. However, *B. bouvardioides* is not known from Guerrero and definitely solving the problem of the ancestry of such putative hybrids will require intensive field work followed by experimental studies.

12. Bouvardia gracilipes B. L. Robinson, Proc. Amer. Acad. Arts Sci. 45: 404, 1910.

Shrubs to 1.5 m; seasonal branches glabrous or distally white-papillose-puberulent with trichomes to 0.05 mm long. Leaves with petioles 0.5-3.5 mm long; blades ovate to ovate-lanceolate, 2-9 cm long, 1-4.4 cm broad, membranous, glabrous above, often puberulent or pilosulous below on the main veins (and marginally) with trichomes 0.05-0.5 mm long, otherwise glabrous, the secondaries 6-10, pinnate, often brochidodrome, the reticulation most conspicuous below, imparting a minutely varicose appearance to the blade above. Inflorescences 5 to 50-flowered, pseudoaxillary, the floriferous branchlets less than 7 cm long (including flowers), less than 1 mm broad, leafless (only a stipule-sheath present at the nodes), with only 1 or 2 very short internodes below the peduncle. Flowers with pedicels 5-22 mm long (at least a few pedicels 8 mm or more) and less than 0.5 mm broad; floral cup minutely papillose-puberulent with trichomes to 0.05 mm long or glabrate; calyxlobes deltoid to lanceolate, 0.5-2 mm long; corolla tubular, yellow or orange-yellow, externally minutely papillose-puberulent with trichomes to 0.05 mm long, the tube 10-19 mm long, often somewhat pilosulous within just below the middle (but not with a dense, villous ring), the lobes broadly ovate to oblong, 2-4.5 mm long; anthers 1.5-3 mm long, exserted in thrum flowers by 1-2 mm; style glabrate, the branches 0.5-1 mm long. Capsules 3.5-5.5 mm long, 4-7 mm broad; seeds 1.5-2.5 mm broad.

Holotype: Mexico. Nayarit: Tepic, 5 Jan to 6 Feb 1892, Palmer 1971 (GH); isotypes F, US.

Nayarit and northwestern Jalisco; steep, heavily forested stream valleys in the oak zone; growing in cracks and among rocks in stream beds; known to be in flower in November and December.

13. Bouvardia rekoi Standley, N. Amer. Fl. 32: 108, 1921.

Shrubs; seasonal branches glabrous or distally minutely puberulent with trichomes to 0.05 mm long. Leaves with petioles 1-3 mm long; blades ovate-lanceolate, rounded at the base, 3-6.5 cm long, 0.9-2.7 cm broad, glabrous, 3 to 5-plinerved, the reticulation often prominent below. Inflorescences few-flowered. Flowers with pedicels 6-13 mm long and 0.2-0.3 mm broad; floral cup sparsely pruinose-puberulent or hispidulous with trichomes to 0.05 mm long; calyx-lobes deltoid-acuminate, ca 1 mm long; corolla tubular, externally glabrate, the tube 10-19 mm long, a

villous ring within near the base, the lobes oblong or oblong-lanceolate, 2.5-4 mm long; anthers 1.5-3 mm long, exserted in thrum flowers by 1-4 mm; style glabrate, the branches 1-1.5 mm long.

Holotype: Mexico. Oaxaca: Cafetal Montecristo (Cerro Espino), 1000 m, 7 Dec 1917, Reko 3650 (US 867149).

Known only from the type collection.

14. Bouvardia oaxacana Standley, Jour. Wash. Acad. Sci. 13: 7, 1923.

Herbs, perennial or suffrutices; stems simple or sparsely branched, slender, distally puberulent with white trichomes 0.05-0.3 mm long. Leaves with petioles 0-2.5 mm long; blades broadly ovate to ovate-lanceolate, basally rounded, 3.4-6.7 cm long, 1.3-3.8 cm broad, glabrate or sparsely white-puberulent with trichomes 0.1-0.5 mm long (often primarily along the margin), 5-plinerved, the reticulation obscure above, visible but inconspicuous below. Inflorescences often more than 30-flowered, subcapitate. Flowers with pedicels 0.5-4 mm long and 0.5 broad; floral cup usually densely hirtellous; calyx-lobes lanceolate to elliptic- or linear-lanceolate, 2-9 mm long, 1-2 mm broad; corolla tubular, red, externally glabrous or sparsely hirtellous, the tube 10-17 mm long, villous toward the base within but lacking a villous ring, the lobes mostly oblong-lanceolate, 3-6 mm long; anthers 2-3 mm long, exserted by 2-6 mm in thrum flowers; style glabrate, the branches 1-2 mm long.

Holotype: Mexico. Oaxaca: Distr Juquila, betw Santa Cruz & El Aguacate, 500 m, 24 Dec 1921, Conzatti 4513 (US 1110842); isotype GH.

Known only from the type collection.

15. Bouvardia quinquenervata Standley, N. Amer. Fl. 32: 108, 1921.

Shrubs; seasonal branches rather elongate, distally hirtellous with trichomes 0.05-0.3 mm long. Leaves with petioles 1-5 mm long; blades broadly ovate to ovate- or elliptic-lanceolate, basally obtuse to rounded or cordate, 2.6-5.9 cm long, 1.3-3.7 cm broad, glabrate above, obscurely puberulent below on the main veins with trichomes to 0.1 mm long, 5-plinerved, the reticulation visible above, prominent below. Inflorescences usually more than 50-flowered. Flowers with pedicels 1.5-6 mm long, to 0.5 mm broad; floral cup rather densely hirtellous; calyx-lobes linear-subulate, 2-6 mm long, 0.3-1 mm broad; corolla tubular to virtually salver-form, violet or lavender, externally sparsely hirtellous (mainly toward the base) with trichomes 0.1-0.2 mm long, the tube 4.5-8.5 mm long, rather densely villous in the lower half (the pubescence not organized into a villous ring), the lobes oblong to oblong-lanceolate, 2.5-4 mm long; anthers 2-3.5 mm long, exserted in both pin and thrum flowers by 1-5.5 mm; style somewhat hirtellous or villosulous on the lower half. Capsules 3-4.5 mm long, 2.4-4 mm broad.

Holotype: Mexico. Chiapas: San Bartolomé, 22 March 1904, Goldman 769 (US 470574).

Southern Chiapas; pine forests on volcanic slopes; ca 1400 m; known to flower December through March.

Based on the many-flowered inflorescences, the short lavender corollas and stamens exserted in both pin and thrum flowers, *B. quinquenervata* appears more closely related to specimens of *B. bouvardioides* from Chiapas and Guatemala than to any member of the subg. *Bouvardiastrum*.

II. Subg. Bouvardioides Schlecht., Linnaea 26: 58, 1854.

Shrubs or suffrutices; seasonal branches opposite, glabrous or pubescent. Leaves opposite, usually petiolate; blades glabrous or pubescent, the secondaries pinnate, obscure or rarely subpalmate, the reticulation obscure or inconspicuous. Inflorescences 1- or several (to 15)-flowered (when several-flowered, each partial inflorescence composed of only 1 flower). Flowers pedicellate or sessile, ± erect; calyx-lobes free to the floral cup or rarely connected basally by a calyx-tube; corolla salverform (lobes spreading at an angle of 90°), white, externally glabrous or pubescent, the tube internally sparsely pilose throughout or the pubescence limited to the upper half (never limited to the lower half), less often glabrate internally; anthers in both pin and thrum flowers included or only the tips protruding; style glabrate or more often minutely papillose-pubescent (at least on the distal half), the branches 1-7.5 mm long.

Type: Bouvardia longiflora (Cav.) H.B.K.

a. Flowers sessile or subsessile on a branch terminus (rarely with pedicels to 1 mm long), usually solitary (if inflorescences several-flowered then the leaf-blades conspicuously villous beneath toward the base with trichomes to 1 mm long and the floral cup villous-tomentose or else the flowers with a calyx-tube ca 2 mm long extending beyond the floral cup).

b. Flowers solitary (if inflorescences 3 or more-flowered then the floral cup villous-tomentose with trichomes to 1.5 mm long and the leaf-blades conspicuously villous below toward the base); calyx-lobes free to the floral

cup.

aa. Flowers typically at least short-pedicellate; inflorescences often 3- or more-flowered (if flowers solitary, the leaf-blades less than 9 mm broad and the plants often low, dense shrubs of xerophytic habit).

d. Petioles (0.5-)3-12 mm long; leaf-blades usually broader than 9 mm, the secondaries evident; inflorescences 3 to 15-flowered.

 dd. Petioles 0-3(-4.5) mm long; leaf-blades usually less than 9 mm broad, the secondaries usually obscure; inflorescences 1 to 9-flowered.

ff. Typically not xerophytes, the branches not at all spinescent; leaf-blades 0.9-7 cm long, glabrate or rarely papillose-puberulent with trichomes to 0.3 mm long; inflorescences often 3 to 9-flowered, the flowers occasionally solitary; calyx-lobes 2-32 mm long.

16. Bouvardia Longiflora (Cav.) H.B.K., Nov. Gen. Sp. Pl. 3: 386, 1820.

Aeginetia longiflora Cav., Anal. Ci. Nat. 3: 130, t. 28, fig. 1, 1801; Ic. 6: 51, t. 572, fig. 1, 1801.

Bouvardia longiflora var. latifolia Martens & Galeotti, Bull. Acad. Bruxelles 11(1):236, 1844. (Holotype Galeotti 2659 BR)

Houstonia longiflora (Cav.) A. Gray, Proc. Amer. Acad. Arts Sci. 4: 314, 1860.

Shrubs to 1.6 m; seasonal branches ascending, glabrous or distally white-papillose-hirtellous with trichomes to 0.2 mm long, often short and slender and herbaccous. Leaves with petioles to 10 mm long; stipular processes lanceolate or slender-subulate, 2.5-10 mm long; blades lanceolate or occasionally ovate- or elliptic-lanceolate, 1.5-5.7 cm long, 0.5-2.2 cm broad, glabrous or infrequently white-puberulent with trichomes 0.05-0.3 mm long, the secondaries 4-12, pinnate. Flowers solitary, sessile or subsessile (pedicels to 1 mm long); floral cup glabrate or rarely densely puberulent with white trichomes 0.1-0.3 mm long; calyx-lobes linear to linear-lanceolate or linear-oblanceolate, rarely more broadly oblanceolate or ± elliptic, (2.5-)6-26 mm long; corolla glabrous externally or rarely sparsely puberulent with trichomes to 0.3 mm long, the tube 3.5-8.5 cm long, internally sparsely pilose throughout, the lobes 8-28 mm long; anthers 3-5 mm long; ovary 2-5 mm long, the style glabrate or pruinose-puberulent, the branches 2-6 mm long. Capsules 8-12.5 mm long, 7-12 mm broad; seeds 1.5-4 mm broad.

Holotype: Mexico: betw Queretaro & Guanajuato, Oct (MA, not seen). The description is based on a specimen in the herbarium of L. Née without reference to the collector.

Aguascalientes, Jalisco and San Luis Potosi to Puebla and Oaxaca; occasional on rhyolitic or basaltic hillsides or steep roadcuts at elevations of 2000-4000 m; sometimes associated with xerophytic plants in arid or semiarid habitats but more frequently occurring in mesic woodlands of oak and pine; flowering most commonly from May through August.

Two collections of *B. longiflora* from Puebla, *Purpus 1249* (GH, MO) from Tehuacan and *Purpus* 3327 (MO, UC) from the vicinity of San Luis Tultitlanapa, are distinguished by their puberulent leaves, densely puberulent floral cups and shorter calyx-lobes (2.5-6 mm long). At first I thought these formed a distinct

subspecies. However, other collections of "typical" B. longiflora, Purpus 3323 (F) & 3326 (GH, MO), from the vicinity of San Luis Tultitlanapa were subsequently seen and cast doubt on the geographical separation of the puberulent forms. Additional collecting is needed to elucidate their status.

17. Bouvardia langlassei Standley, N. Amer. Fl. 32: 110, 1921.

Shrubs to 1.5 m; seasonal branches distally villous with trichomes 0.2-1 mm long, often short and herbaceous. Leaves with villous petioles to 7 mm long; stipular processes 1-3.5 mm long, often pluriaristate; blades obovate or oblanceolate to ovate or ovate-lanceolate, 1.2-5.2 cm long, 0.5-2.8 cm broad, villous (particularly beneath toward the base) with white trichomes 0.3-1 mm long, the secondaries 4-10, pinnate or infrequently \pm plinerved. Flowers solitary or 3-11 on a seasonal branch, sessile or subsessile (pedicels to 1 mm); floral cup densely white-villous with trichomes 0.5-1.5 mm long; calyx-lobes linear or slender-lanceolate, 2.5-9 mm long; corolla distally sparsely villous externally with slender trichomes 0.3-1.5 mm long or glabrous (when glabrous, the inflorescence typically several-flowered), the tube 3.5-6.6 cm long, internally glabrate or sparsely pilose throughout, the lobes 6-14 mm long; anthers 3-4 mm long; ovary 1-3 mm long, the style glabrate, the branches 1.5-3.5 mm long.

Holotype: Mexico. Guerrero: Testla (Yextla), 45 km W of Chilpancingo, 1500 m, 8 June 1899, Langlassé 1049 (US); isotypes F (fragment), G, GH, P; photo US.

Guerrero and northwestern Michoacan; infrequent; mountain slopes in rocky soil, often under semiarid conditions; 1000-2000 m; known to be in flower in June.

18. BOUVARDIA ERECTA (DC.) Standley, N. Amer. Fl. 32: 110, 1921.

Catesbaea erecta DC., Prodr. 4: 401, 1830.

Hedyotis spinescens Sessé & Mociño, Fl. Mex. 22, 1891. (Type Sessé & Mociño s.n. MA, not seen)

Bouvardia flos-joannis Schumann in Loesener, Bull. Herb. Boiss. 3: 621, 1895. (Type Seler 846 GH)

B. flos-joannis var. latifolia Loesener, Repert. Sp. Nov. 18: 358, 1922. (Type Endlicher 1966 W, not seen)

Shrubs to 1.2 m; seasonal branches glabrous or papillose-hispidulous with white trichomes to 0.2 mm long, \pm herbaceous, becoming woody and pseudospinescent. Leaves often pseudofasiculate by virtue of crowding and the development of axillary buds which produce leaves but fail to elongate; petioles to 2.5 mm long; stipular processes slender-deltoid, 0.5-2 mm long; blades lanceolate or linear to elliptic-lanceolate or oblanceolate, 3.5-12(-18) mm long, 1-4.5 mm broad, chartaceous, glabrous or white-papillose-puberulent with trichomes to 0.2 mm long, the secondaries obscure. Flowers solitary (rarely 3 terminating a branchlet); pedicels (0-)1-8 mm long; floral cup glabrous or puberulent with trichomes to 0.2 mm long; calyx-lobes linear to lanceolate or slightly oblanceolate, 1.5-5(-6.5) mm long; corolla white but often lightly suffused with rose, inconspicuously puberulent externally with trichomes to 0.05 mm long or glabrate, the tube 2.5-5.5 cm long, sparsely pilose in the upper half (sometimes densely so at the throat), the lobes

5-12 mm long; anthers 2-4 mm long; ovary 1-2.5 mm long, the style often minutely papillose-puberulent, the branches 1.5-5 mm long. Capsules 4-9 mm long, 4-8.5 mm broad; seeds 2-3 mm broad.

Type: Mexico: Sessé & Mociño s.n. (MA, not seen); pl. 460 of the Calques des dessin... is a drawing of the type.

Puebla; limestone slopes with gray or whitish soil and frequent rock outcrops; often in association with thorn-scrub, cactus and hat palms under arid conditions; 1300-2500 m; flowering from June through early October.

Bouvardia erecta is unique in the subg. Bouvardioides in its adaptation to xeric conditions. The habit is that of a dense, low shrub of scrubby appearance. The branchlets are often pseudospinescent and the leaves small and rather densely crowded.

19. Bouvardia Rosei Standley, N. Amer. Fl. 32: 109, 1921.

Shrubs, the branches minutely puberulent when young. Leaves with petioles ca 1 mm long; stipular processes narrowly lanceolate, 3-5 mm long; blades ovate to elliptic, 2-3.8 cm long, 0.7-2 cm broad, glabrate, the secondaries 4-8, subpalmate (two arising from the midvein slightly below the midpoint of the leaf and the remainder originating together near the base or occasionally all originating near the base). Inflorescences 3 to 5(-7)-flowered. Flowers typically sessile (occasionally with pedicels to ca 1 mm); floral cup pruinose-puberulent; calyx-lobes linear-lanceolate, 4-9 mm long, connected basally by a calyx-tube extending ca 2 mm above the floral cup; corolla glabrate externally, the tube 4-7 cm long, internally sparsely pilose throughout, the lobes 11-15 mm long; anthers 3-4 mm long; ovary ca 1.5 mm long; style moderately papillose-hispid distally, the branches 4-6 mm long. Capsules 6-8 mm long and broad; seeds 2-3 mm broad.

Holotype: Mexico. Durango: Sierra Madre, 16 Aug 1897, Rose 3516 (US); isotype F; photo US.

Sierra Madre of Durango and Sinaloa; infrequent; known to be in flower in August (probably also in September).

- 20. Bouvardia glabra Polakowsky, Linnaea 41: 565, 1877.
- B. glabra var. gracilis Polakowsky, loc. cit. 566. (Type Polakowsky 172 B†, BM, W; photos F, G, TEX)
- B. glabra var. obtusa Loesener, Verh. Bot. Ver. Brandenburg 65: 106, 1923. (Type Seler 2920 B†)

Shrubs to 1.5 m; branches glabrous. Leaves with petioles (2-)3-12 mm long; stipular processes lanceolate or linear-lanceolate, 1.5-6 mm long; blades ovate- or elliptic-lanceolate, 2.5-10.5 cm long, 0.9-4.3 cm broad, glabrous or glabrate, the secondaries 6-12, pinnate. Inflorescences 3 to 7-flowered. Flowers with pedicels (0.5-)2.5-19 mm long; calyx-lobes elliptic to oblanceolate or ± linear, 3.5-17 mm long, (0.5-)1.5-5 mm broad; corolla externally glabrous or rarely minutely puberulent with trichomes to 0.05 mm long, the tube 1.5-4.5(-5.6) cm long, glabrate within, the lobes 5-16 mm long; anthers 2.5-4 mm long; ovary 1.5-3 mm long; style pruinose-puberulent, the branches 1.5-7.5 mm long. Capsules 4-10 mm long, 5-10 mm broad; seeds 2-4.5 mm broad.

Type: Costa Rica: San José, Aug 1875 Polakowsky 337 (B†, F fragment; photos F, G, TEX, US); possibly from cultivated material.

Guatemala, southern Chiapas and Costa Rica; wooded or shrubby slopes or barrancas of volcanic mountains in arid to very mesic (cloud forest) conditions; 1300-3500 m; flowering the year round.

I have seen collections from Honduras perhaps assignable to *B. glabra* but intermediate between *B. glabra* and *B. dolichantha*. Examples of these possibly hybrid specimens are *Hawkes et al.* 2095 (C, G, K), *Molina* 6501 (F) and *Rodriguez* 3124 (F). Additional collecting is needed to ascertain more accurately the distribution of *B. glabra*, *B. dolichantha* and *B. induta* and to look for intermediate forms. These three taxa are a closely related complex in northern Central America and I view the specific status of *B. dolichantha* and *B. induta* as tentative at present.

- 21. Bouvardia induta (Robinson) Standley, N. Amer. Fl. 32: 109, 1921.
- B. longiflora var. induta B. L. Robinson, Proc. Amer. Acad. Arts Sci. 45: 404, 1910.
- B. purpusii Brandegee, Univ. Calif. Publ. Bot. 10: 415, 1924. (Holotype Purpus 9251 UC 223423 †?; isotypes F, GH, MO, US)

Shrubs to 1 m; branches distally rather densely white-hirsute with trichomes to 0.8 mm long or glabrous. Leaves with petioles (0.5-)3-9 mm long; stipular processes subulate, 1-3.5 mm long; blades lanceolate to ovate- or elliptic-lanceolate, (1.5-)2-7.3 cm long, (0.5-)1-2.5 cm broad, conspicuously white-hirsute with trichomes to 1 mm long or glabrous, the secondaries 4-10, pinnate. Inflorescences 3 to 15-flowered. Flowers with pedicels 0.5-2.5(-6) mm long which are densely hirsute to glabrate; floral cup white-hirsute-tomentellous with trichomes to 1 mm long or minutely puberulent (trichomes to 0.05 mm long) or glabrate; calyx-lobes linear to linear-lanceolate or linear-elliptic or slightly oblanceolate, 2.5-16 mm long, 0.5-1(-2) mm broad; corolla externally villosulous or hirsute with trichomes 0.1-0.7 mm long or pruinose- or papillose-puberulent with trichomes to 0.05 mm long, rarely glabrate externally, the tube (3.5-)4.5-8.5 cm long, pilose in the distal half with trichomes to 1 mm long, the lobes 7-22 mm long; anthers 3-5 mm long; ovary 1-2.5 mm long, the style distally minutely puberulent and proximally glabrous, with branches 1-5 mm long.

Holotype: Mexico. Chiapas: June-July 1864-70, Ghiesbreght s.n. (GH). The holotype is one of three collections of B. induta on one herbarium sheet, viz. the one in the middle. The specimens on the left and right are Ghiesbreght 108 and 692 respectively.

Chiapas and adjacent Guatemala; rocky, dry limestone areas in pine forests; 1000-2200 m; flowering March through September.

Some specimens of *B. purpusii* differ from *B. induta* in the glabrescence of all parts (see *Purpus 9252 MO*, UC, US). However, the holotype is a pubescent plant similar to the majority of specimens of *B. induta*. An isotype (F) is a mixed collection, the specimen on the left side of the herbarium sheet being glabrate and the one on the right conspicuously pubescent. The specimens on the right is probably a duplicate of the holotype.

22. BOUVARDIA DOLICHANTHA Loesener, Verh. Bot. Ver. Brandenburg 65: 106, 1923. B. steyermarkii Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 22: 383, 1940. (Holotype Steyermark 29671 F 1043386; photos F, TEX)

Shrubs or low suffrutices; branches glabrous or sparsely papillose- or pruinosepuberulent distally with trichomes to 0.05(-0.3) mm long. Leaves opposite but occasionally crowded and pseudoverticillate; petioles 0.5-3(-4.5) mm long; stipular processes deltoid to lanceolate, 0.5-3 mm long; blades linear or lanceolate to elliptic- or narrowly ovate-lanceolate, 0.9-7 cm long, 1.5-9 mm broad, glabrate or rarely papillose-puberulent with trichomes to 0.3 mm long, the secondaries obscure or 4-6 and pinnate. Inflorescences (1-)3 to 9-flowered. Flowers with pedicels 0.5-5.5 mm long which are glabrous or minutely puberulent; floral cup typically pruinose- or papillose-puberulent with trichomes to 0.05(-0.3) mm long; calyxlobes linear or lanceolate to narrowly elliptic or oblanceolate, 2-11 mm long, 0.5-1.3(-2) mm broad; corolla externally glabrous or sparsely papillose-puberulent with trichomes to 0.05(-0.2) mm long, the tube 1.7-8 cm long, internally glabrate or papillose-puberulent to pilose (trichomes 0.1-1 mm long) in the upper half, the lobes 4-19 mm long; anthers 2-4 mm long; ovary usually subglobose, 1-2 mm long, the style minutely puberulent on the distal two-thirds, with branches 1-5 mm long. Capsules 3.5-8.5 mm long and broad; seeds 2-3.5 mm broad.

Loesener cites Seler 2795 and 2883 without selecting one or the other as the type. I designate Seler 2883 (US 1205579) as lectotype (Guatemala: Dept of Huehuetenango, Distr of Nenton, nr Uaxackanal & toward Quen Santo, 1100 m, 9 July 1896); isolectotypes GH, F (fragment); photos F, G, US from B†.

Guatemala and Honduras; occasional on mountainsides along humid banks in mixed woodlands of oak and pine; 1000-3400 m; flowering May through October.

23. Bouvardia karwinskyi Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 155, 1930.

Shrubs to 1.5 m; seasonal branches glabrate or obscurely hirtellous with trichomes to 0.1 mm long. Leaves opposite but often crowded, sometimes pseudofasciculate by the production of leaves by axillary buds which fail to develop into branches; petioles 0-2 mm long; stipular processes lanceolate, 1.5-5.5 mm long; blades linear to linear-lanceolate or narrowly linear-elliptic, 1.6-5.3 cm long, 0.7-3 mm broad, glabrous, the secondaries obscure. Inflorescences 1 to 5-flowered. Flowers with pedicels 0.5-6 mm long which are glabrous; floral cup glabrous, calyx lobes linear, 12-32 mm long, 0.5-1.5 mm broad; corolla glabrous externally, the tube 3.5-6.2 cm long, sparsely pilose in the upper half, the lobes 7-13.5 mm long; anthers 3-3.5 mm long; ovary turbinate or subcylindrical, 2-3.5 mm long, the style papillose-puberulent (particularly distally) with trichomes to 0.05 mm long, with branches 1-2 mm long.

Holotype: Mexico: betw Victoria & Río Blanco, 1842, Karwinsky 312 (LE); isotype F (fragment).

I have been unable to learn the state(s) in which the type and other specimens of B. karwinskyi were collected; flowering July through October.

III. Subg. Bouvardia Schlecht., Linnaea 26: 58, 1854.

Shrubs, suffrutices or perennial herbs; seasonal branches opposite or verticillate, pubescent to glabrous. Leaves 3 to 4(-6)-nate at some or all of the nodes, petiolate or sessile; blades conspicuously pubescent (mostly below) to glabrous, the secondaries pinnate, arcuate, less frequently obscure, the reticulation obscure to prominent. Inflorescences few to many-flowered; partial inflorescences 3- or more-flowered. Flowers pedicellate or virtually sessile; calyx-lobes free to the floral cup; corolla tubular to salverform (lobes spreading 10-90°), red, less frequently lavender, rose, violet-blue or pink, externally pubescent or glabrous, the tube internally pilose or villous in the lower half (rarely glabrate) or the pubescence organized into a villous ring near the base; anthers included (rarely exserted) in pin flowers; included or often exserted in thrum flowers; style usually glabrate, the branches 0.5-3 mm long.

- a. Corolla externally pubescent, rarely obscurely pruinose-puberulent or glabrate but then the leaves obovate and 5 to 6-nate at some of the nodes.
 - b. Leaves not more than 4-nate, the blades typically neither obovate nor mucronulate; corolla-tube puberulent externally with trichomes usually 0.1-0.4 mm long, internally with a villous ring toward the base.
 - c. Well-branched shrubs or low suffrutices (occasionally the stems simple and herbaceous but broader than 1.5 mm at the midpoint); leaves at least short-petiolate, the blades having a length/width ratio of 1.5/1 to 19/1 and most often not linear, the secondaries usually apparent
 - cc. Herbaceous or suffrutescent perennials, the stems 1-1.5 mm broad at the midpoint, simple or sparsely branched distally; leaves often sessile or subsessile (occasionally short-petiolate), the blades linear, with a length/width ratio of 12/1 to 50/1, the secondaries obscure25. B. tenuifolia
- aa. Corolla externally glabrous.

 d. Seasonal branches distally villosulous or hirsute with trichomes 0.2-2 mm long; leaves short-petiolate or subsessile (petioles 0.5-3 mm long), the blades often conspicuously pubescent (particularly below) with trichomes 0.2-1.1 mm long (the pubescence either coarse and yellowish or villous and white); corolla red, the tube 10-27 mm long; inflorescences with fewer than 60 flowers and often subcapitate.
 - e. Slender shrubs or suffrutices, the branches angular or terete in cross-section and less than 3 mm broad at the midpoint; leaf-blades various (often ovate-lanceolate), white-villous-pubescent below, the secondaries 4-14 (often fewer than 12); calyx-lobes usually less than 5.5 mm long; anthers exserted 1-3 mm in thrum flowers, included in pin flowers.

 - ff. Corolla salverform, the tube villous internally toward the base but lacking a definite villous ring, the lobes frequently, 2.2 mm broad or more, spreading at 90° ________28. B. viminalis

- dd. Seasonal branches distally glabrous or puberulent with trichomes to 0.1 mm long; leaves entirely sessile or conspicuously petiolate (at least some of the petioles exceeding 4 mm), the blades glabrous or sparsely hirtellous with trichomes to 0.3 mm long; corolla deep-rose, lavender, violet-blue, pink or red (when red the inflorescences more than 60-flowered and not subcapitate), the tube 2-19 mm long.
 - g. Leaves sessile, the blades linear, having a length/width ratio of 4/1 to 20/1, the secondaries obscure; inflorescences 3 to 20-flowered30. B. rosea
- 24. Bouvardia ternifolia (Cav.) Schlecht., Linnaea 26: 98, 1854.

Ixora ternifolia Cav., Ic. 4: 3, t. 305, 1797.

I. americana Jacquin, Hort. Schönbr. 3: 4, 1798. (Based on I. ternifolia)

Houstonia coccinea Andrews, Bot. Repos., pl. 106, 1800. (Illustration is taken as the type) Bouvardia triphylla Salisbury, Parad. Lond., pl. 88, 1807. (Based on I. ternifolia)

- B. linearis H.B.K., Nov. Gen. Sp. Pl. 3: 383, 1819. (Type Humboldt & Bonpland s.n. P, not seen; photos F, P, TEX, US).
- B. angustifolia H.B.K., loc. cit. 384. (Type Humboldt & Bonpland s.n. F, P not seen, US; photos F, P, TEX, US)
- B. hirtella H.B.K., loc. cit. (Type Humboldt & Bonpland s.n. P, not seen; photos F, P, TEX, US)
- B. jacquinii H.B.K., loc. cit. 385, 1820. (Based on I. americana)

B. coccinea (Andrews) Link, Enum. Hort. Berol. 1: 139, 1821.

- B. quaternifolia DC., Prodr. 4: 365, 1830. (Type Alaman s.n. G-DC, not seen; photo IDC)
- Carphalea pubiflora Sessé & Mociño ex DC., loc. cit. (As synonym of B. quaternifolia) Bouvardia jacquinii var. β exogyna DC., loc. cit. (Based on a plant grown in Salm-Dyck's garden; type G-DC, not seen; photo IDC)
- B. jacquinii var. γ ovata DC., loc. cit. (Based on "Bouvardia triphylla var. β Salisb.," the supposedly broader-leafed form, the type of which is Salisbury's pl. 88)
- B. splendens Graham, Bot. Mag., pl. 3781, 1840. (Based on greenhouse-grown plants; K)

B. triphylla var. splendens (Graham) Lindley, Bot. Reg. 26: t. 37, 1840.

- B. tolucana Hooker & Arnott, Bot. Beechey Voy. 427, 1840. (Type Andrieux 332 K, W)
- B. quaterniflora Steudel, Nomen. Bot. ed. 2, part 1, 300, 1841, as synonym of Carphalea publiflora; probably a mistake for B. quaternifolia DC.
- B. scabrida Martens & Galeotti, Bull. Acad. Bruxelles 11(1): 237, 1844. (Holotype Galeotti 2624 BR)
- B. hypoleuca Bentham, Pl. Hartw. 288, 1848. (Type Hartweg 1605 K; photo MICH)
- B. glaberrima Engelmann in Wislizenus, Tour N. Mex. 106, 1848. (Type Wislizenus 161 GH, MO)
- B. ovata A. Gray, Pl. Wright. 5: 67, 1853. (Type Wright 1117 GH, MO, US)
- Aeginetia hyssopifolia Willd. ex Schlecht., Linnaea 26: 60, 1854. (As synonym of Bouvardia angustifolia)

Bouvardia tenuiflora Schlecht., loc. cit. 97. (Type B†)

- B. houtteana Schlecht. ex Planchon, Fl. Serres 10: 149, t. 55, 1855. (Illustration is taken as the type)
- B. hirtella var. quaternifolia (DC.) Rothrock in Wheeler, Rept. U.S. Geogr. Surv. 6: 137, 1879.
- B. triphylla var. angustifolia (H.B.K.) A. Gray, Syn. Fl. N. Amer. 1(2): 24, 1884.
- B. ternifolia var. angustifolia (H.B.K.) B. L. Robinson, Proc. Amer. Acad. Arts Sci. 45: 405, 1910.
- B. endlichii Loesener, Repert. Sp. Nov. 18: 357, 1922. (Type Endlicher 176a B†; photos F, G, TEX, US).
- B. orizabensis Standley, Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 334, 1931. (Holotype Botteri 604 P; isotypes F fragment, G)

Shrubs or suffrutices or perennial herbs to 1.5 m, the branches sparsely to rather densely papillose-hispidulous when young with white trichomes 0.1-0.3 mm

long. Leaves with petioles 0.5-12 mm long; blades extremely variable (linear, lanceolate, elliptic, ovate, obovate) though most often elliptic-lanceolate, 1-11 cm long, 0.1-3.1 cm broad, glabrate to densely papillose-hispidulous or villosulous with white trichomes variously 0.05-1 mm long, the secondaries 4-12 (often obscure in narrow, linear leaves), the reticulation apparent or obscure. Cymes 3 to 40flowered, sometimes subcapitate. Flowers with pedicels 1-15 mm long; floral cup sparsely to densely papillose-hispidulous; calyx-lobes lanceolate to linear, 2-10 mm long; corolla tubular, salmon-red or orange-red or scarlet, externally pubescent with papillose, white, red-tipped trichomes 0.1-0.4 mm long (rarely obscurely puberulent with trichomes 0.05 mm long or less or villosulous with trichomes to 0.8 mm long), the tube 9-35 mm long, typically with a villous ring internally toward the base, the lobes ovate to oblong, 1.5-3.5(-5) mm long, spreading up to 60°, internally white-pruinose-puberulent; anthers 2-4 mm long, white or red, included by 1-4 mm or the tips protruding; ovary 1-2.5 mm long, the style-branches red, 1-2.5 mm long. Capsules 4.5-9 mm long, 5-10.5 mm broad, glabrous or sparsely papillose-hispid; seeds 2-3.5 mm broad.

The original description of *Ixora ternifolia* was based on a plant growing in the Royal Botanical Garden of Madrid, the seed having been sent from Mexico. The illustration is taken as the type.

Southwestern Texas and New Mexico and southeastern Arizona to Oaxaca and southern Vera Cruz; the most common species of *Bouvardia*; frequent in desert and mesic, montane habitats; 800-3000 m; flowering mostly from late February through October.

In examining type material of *B. scabrida*, *Galeotti* 2624, specimens at P and W (and photos A, F, MICH, TEX) were found to be *B. viminalis*. However, the specimen at BR is *B. ternifolia* and *Galeotti* 2624 is thus a mixed collection. As the original publication clearly describes the BR specimen, it is regarded as the type of *B. scabrida*. The "isotypes" and "phototypes" discussed are merely additional specimens of *B. viminalis*.

Standley (Publ. Field Mus. Nat. Hist., Bot. Ser. 8: 334, 1931) considered B. orizabensis to be a "well marked" species "related clearly to B. bouvardioides." Examination of type material, however, showed B. orizabensis to be synonymous with B. ternifolia. Confusion may have arisen because of the obscurity of the pubescence, particularly of the corolla, on the F and P type specimens of B. orizabensis. It is worthy of mention, however, that the external pubescence of the G specimen is similar to that of typical specimens of B. ternifolia and may be from another plant. Even if Botteri 604 represents a mixed collection, all the specimens involved are still referable to B. ternifolia.

25. Bouvardia tenuifolia Standley, N. Amer. Fl. 32: 104, 1921.

Herbs, often suffrutescent toward the base; stems simple or sparsely branched distally, 1-1.5 mm broad at the midpoint, glabrous or distally minutely puberulent to villosulous (white trichomes 0.05-0.7 mm long). Leaves with petioles 0-3 mm long; blades linear, 2-9.5 cm long, 0.7-4.5 mm broad, glabrous or pubescent with trichomes similar to those of the distal portion of the stem, the secondaries and

reticulation obscure. Cymes 3 to 25-flowered, often subcapitate. Flowers with pedicels 0.5-6 mm long; calyx-lobes narrowly deltoid to subulate or linear, 1-3 mm long; corolla tubular, red, externally pubescent with papillose, white, red-tipped trichomes 0.1-0.4 mm long, the tube 7-26 mm long, a villous ring within near the base, the lobes ovate or elliptic, 1.5-5 mm long; anthers 2-4 mm long, included by 1-6 mm or the tips protruding; ovary 1-1.5 mm long, the style-branches 0.5-2 mm long.

Holotype: Mexico. Jalisco: grassy hillsides nr Guadalajara, Oct 1899, Pringle 2292 (US); isotypes A, BM, BR, F, G, LE, M, MICH, MO, MSC, P, UC, W.

Sinaloa and western Durango to northern Jalisco; found in various habitats: precipitous slopes with pine and oak, open slopes in palm-oak country, grassy hill-sides, gravelly banks of ravines, dry hills; 150-2700 m; flowering July through December.

Intergradation occurs between *B. tenuifolia* and *B. ternifolia* where their ranges overlap, viz. the Western Sierra Madre from extreme western Durango and eastern Sinaloa to Nayarit and northwestern Jalisco. The shaky separation of the two species by a combination of leaf and habit characters may prove untenable in the light of future collecting.

26. Bouvardia obovata H.B.K., Nov. Gen. Sp. Pl. 3: 385, 1820.

Hedyotis fruticosa Sessé & Mociño ex DC., Prodr. 4: 365, 1830. (Type Sessé & Mociño s.n. BM, F)

Herbs or suffrutices to 1.3 m; stems glabrous or sparsely papillose-puberulent (most noticeably at the nodes and on the extreme distal portion) with white trichomes to 0.1 mm long. Leaves 3 to 6-nate (at least one or two nodes 5- or 6-nate); petioles 0-7 mm long; blades obovate to elliptic, 3.5-13 cm long, 0.9-3.8 cm broad, often mucronulate, glabrate, the secondaries 6-12, the reticulation apparent below, often subobscure above. Cymes 10 to 60-flowered. Flowers with pedicels 0.5-12 mm long; calyx-lobes lanceolate, 2-4 mm long; corolla tubular, red, externally minutely papillose-puberulent with white, red-tipped trichomes to 0.05 mm long, the tube 10-32 mm long, internally glabrate or somewhat villosulous toward the base (not with a villous ring), the lobes ovate to elliptic or oblong, 2-5 mm long, flared up to 30°; anthers 2.5-3.5 mm long, included by 1-8 mm or the tips protruding; ovary 1-2 mm long, the style-branches 1-3 mm long. Capsules 5.5-9 mm long, 6-10 mm broad, glabrous; seeds 2-3.5 mm broad.

Type: Mexico. Distrito Federal: betw Chapultepec & Tezcoco, "1200 hex.?", June 1803-04, Bonpland s.n. (P).

Occuring sporadically in Nayarit, Mexico State, the Federal District, Morelos and Oaxaca; wooded slopes and barrancas of volcanic mountains; rolling grassy hills in oak forests with a few pines; 1000-2150 m; flowering June through September.

- 27. Bouvardia Leiantha Bentham, Pl. Hartw. 85, 1841.
- B. corymbosa Örsted, Vid. Medd. Nat. For. Kjöbenh. 1852: 46, 1852. (Type probably Örsted 11039 C)

Shrubs to 1.5 m, the branches hirtellous or villosulous with white trichomes 0.2-1 mm long when young. Leaves with petioles to 3 mm long; blades ovate to

ovate- or elliptic-lanceolate, 1.5-7.5 cm long, 0.7-3.5 cm broad, sparsely to densely villosulous (particularly below) with white trichomes 0.3-1 mm long, the secondaries 6-14, the reticulation often prominulous below. Cymes 6 to 45-flowered, often subcapitate. Flowers with pedicels 1-6 mm long; calyx-lobes lanceolate or elliptic-lanceolate to linear or subulate, 2-5.5 mm long; corolla tubular, deep red, glabrous externally, the tube 10-19 mm long, often with an internal villous ring toward the base, the lobes ovate to elliptic or elliptic-lanceolate, 1.5-3.5 mm long, 0.8-2.2 mm broad, spreading up to 45°; anthers 1.5-2 mm long, exserted 1-3 mm in thrum flowers; ovary 1-1.5 mm long, the style-branches 1-2 mm long. Capsules 2.5-5.5 mm long, 3.5-6 mm broad, glabrous; seeds 1.5-2 mm broad.

Type: Guatemala: in fields nr Tejar & Chimaltenango, July-Aug 1841, Hartweg 583 (GH, K, P, W, photo US from B†).

Chiapas to Nicaragua; rocky, open or bushy, moist or dry hillsides in oak-pine forests; sometimes growing in dense tropical forests at lower elevations; 400-4000 m; apparently flowering the year round.

28. Bouvardia viminalis Schlecht., Linnaea 26: 120, 1854.

Shrubs or suffrutices to 1 m; branches villosulous when young with slender white trichomes 0.2-1 mm long. Leaves spreading, often arcuate and ± conduplicate; petioles to 3 mm long; blades ovate-lanceolate, 1.5-5.7 cm long, 0.3-2.6 cm broad, villosulous (particularly below) with white trichomes 0.2-1 mm long, the secondaries 4-13, the reticulation prominulous to obscure. Cymes 7 to 35-flowered, often subcapitate. Flowers with pedicels 0-4 mm long; calyx-lobes lanceolate or elliptic-lanceolate or linear, 1.5-5.5 mm long, somewhat villosulous or hirtellous; corolla salverform, externally pinkish-red and glabrous, the tube 10-20 mm long, internally villosulous toward the base but lacking a villous ring, the lobes typically 4 but occasionally 5 on the same plant, ovate to elliptic or oblong, 2-6.5 mm long, 1-5 mm broad, internally scarlet, flared at ca 90°; anthers 1.5-2.5 mm long, yellowish-white, exserted 1-2 mm in thrum flowers; ovary 1-2.5 mm long, the style-branches 1-2.5 mm long, pink or white. Capsules 3-6.5 mm long and broad, sparsely hirtellous; seeds 1.5-2 mm broad.

Type: Schiede s.n. (B†). I designate Pringle 4888 (MO) as neotype (Oaxaca: Monte Alban, 6000 ft, 4 Sept 1894); isoneotypes BM, BR, F, GH, M, MSC, P, UC, US, W.

Oaxaca and southern Peubla; rocky, open hillsides in sandy soil; sometimes in association with Agave, Karwinskia, Croton and cactus; flowering June through March.

29. Bouvardia scabra Hooker & Arnott, Bot. Beechey Voy. 427, 1840.

Herbs to 1 m, often woody toward the base; stems often simple and tetragonal, 3-4 mm broad at the midpoint, hirsute with yellow trichomes 0.3-2 mm long for virtually the entire length. Leaves with petioles to 3 mm long; blades ovate or rhombic-ovate to elliptic-lanceolate, 2.5-9.8 cm long, 0.7-4.7 cm broad, chartaceous or subcoriaceous, yellowish-hirsute with trichomes 0.2-1.1 mm long (often concentrated below along the main veins), the secondaries (8-) 12-22, raised below, the

reticulation often prominent below. Cymes 15 to 60-flowered, often subcapitate. Flowers with pedicels 0.5-7 mm long; calyx-lobes subulate, suffused with red, hispidulous, (3-)5.5-12 mm long, often spreading; corolla salverform, red, glabrous externally, the tube 10-27 mm long, rather densely villous internally toward the base but rarely with a villous ring, the lobes ovate, 2.5-8 mm long, spreading to 90°; anthers 1-2.5 mm long, included by 2-8 mm; ovary 1-2.5 mm long, the style-branches 1-2 mm long.

Type: Mexico. Nayarit: betw San Blas & Tepic, Sinclair s.n. (K).

Nayarit and Jalisco; rocky mountainsides, wooded ravines, slopes of barrancas; in oak zone or sometimes in tropical deciduous forests; 900-1700 m; flowering August through January.

- 30. Bouvardia Rosea Schlecht., Linnaea 26: 116, 1854.
- B. violacea Rzedowski, Ciencia (Méx.) 19:82, 1959. (Holotype Rzedowski 7680 MEXU, not seen; isotype ENCB)

Herbs to 0.5 m; stems often simple, green, distally compressed, 1-1.5 mm broad at the midpoint, glabrate or pruinose- or papillose-puberulent with white trichomes to 0.1 mm long. Leaves ascending, sessile; blades linear, 2-10 mm long at the lower nodes, to 40 mm long at the upper nodes (except immediately subtending the inflorescence), 0.5-3 mm broad, chartaceous, glabrous or hirtellous with white trichomes to 0.3 mm long, the secondaries and reticulation obscure. Cymes 3 to 20-flowered. Flowers with pedicels 0.5-5 mm long; floral cup glabrous; calyxlobes lanceolate or elliptic-lanceolate, 1-4 mm long; corolla salverform, rose or violet-blue or clear pink, glabrous externally, the tube 5-19 mm long, internally often villous toward the base but lacking a villous ring, the lobes ovate or elliptic-lanceolate or oblong, 2.5-6 mm long, spreading at 90°; anthers 1-2 mm long, exserted 1-2 mm in thrum flowers; ovary turbinate, 1-1.5 mm long, the style-branches 0.5-2 mm long.

Type: Mexico. Hidalgo (?): nr San José del Oro, Schiede s.n. (B†). I designate McVaugh 14819 (MICH) as neotype (Guanajuanto: 22 mi W of Xichu, rd from Xichu to San Luis de la Paz, 2300 m, 14 June 1957).

San Luis Potosi, Guanajuato, Queretaro and Hidalgo; rhyolitic and andesitic hillsides in pine-oak forests; sometimes in dry habitats; 1800-2800 m; flowering April through June.

31. Bouvardia Bouvardioides (Seemann) Standley, N. Amer. Fl. 32: 102, 1921. Hedyotis bouvardioides Seemann, Bot. Voy. Herald 296, 1856.

Houstonia bouvardioides (Seemann) Bentham & Hooker, Gen. Pl. 2: 60, 1873.

Bouvardia pallida Standley, Jour. Wash. Acad. Sci. 14: 245, 1924. (Holotype Standley 22977 US; isotype GH)

Shrubs to 5 m, often slender and clambering, the branches pruinose-puberulent or hirtellous when young with white trichomes to 0.1 mm long. Leaves with petioles (2)4-15 mm long; blades ovate- or elliptic-lanceolate, 2.5-11.5 cm long, 0.7-4.5 cm broad, thinly membranous, glabrate or sparsely appressed-hirtellous with white trichomes to 0.3 mm long (often confined to the main veins below), the secondaries 8-14, the reticulation prominulous below. Cymes typically more than

60-flowered. Flowers with pedicels 1-7 mm long; calyx-lobes linear to lanceolate, 1.5-6 mm long; corolla tubular to somewhat salverform, red or lavender, glabrous externally, the tube 2-18 mm long, internally somewhat villous toward the base (but lacking a definite villous ring), the lobes rather narrowly oblong or elliptic-lanceolate, 2.5-6 mm long, 1-3 mm broad; anthers 1.5-2.5 mm long, exserted by 1-8 mm in pin and thrum flowers; ovary 1-1.5 mm long, the style branches 1-2 mm long. Capsules 2-3 mm long, 2.5-3.5 mm broad, hirtellous with white trichomes to 0.2 mm long; seeds 0.4-0.8 mm broad.

Type: Mexico. Durango (?): Sierra Madre, Seemann s.n. (GH).

A disjunct pattern of distribution is evident: one center of dispersal being in the Western Sierra Madre of Mexico at lower elevations from Durango and Sinaloa to northwestern Jalisco, the other from southern Chiapas to El Salvador. This species occupies diverse habitats at elevations of 300-2000 m and flowers from October to April.

Standley (Jour. Wash. Acad. Sci. 14: 245, 1924) treated the Central American component of this species as a separate species, *B. pallida*, reserving the name bouvarioides for plants of the Western Sierra Madre of Mexico. Although the two groups are apparently widely disjunct geographically, the characters reputedly distinguishing them (corolla size and color) completely break down on careful scrutiny.

EXCLUDED AND DOUBTFUL SPECIES

- 1. Bouvardia alexanderae A. Carter, Madroño 13: 142, fig. 1 & 2, 1955 (Holotype Carter 2577 UC 985926, not seen; isotype F). Carter (loc. cit. 144) recognized that B. alexanderae has wingless, angular seeds but still felt it to be best placed in Bouvardia in the section "having large, white, salverform corollas with long tubes" (subg. Bouvarioides?). However, based on total morphology, choromosome number (n = 13) and geographical location, I believe B. alexanderae to have closest affinity with Baja California species of Hedyotis subg. Edrisia such as H. saxatalis Lewis and H. brevipes (Rose) Lewis. = Hedyotis alexanderae (A. Carter) W. H. Lewis.
- 2. B. chlorantha Bertoloni ex Schultes & Schultes f., Mant. Syst. Veg. 3: 116, 1827, apparently based on a specimen in Bertoloni's herbarium (not seen); the description is not adequate for determination.
- 3. B. coccinea (Aublet) A. Richard, Mém Soc. Hist. Nat. Paris 5: 272, 1834, not B. coccinea (Andrews) Link (Enum. Hort. Berol. 1: 139, 1821). = Nacibea coccinea Aublet = Manettia coccinea (Aublet) Willd., fide Standley, N. Amer. Fl. 32: 97, 1921.
- 4. B. deamii Donn. Sm., Bot. Gaz 49: 445, 1910 (Holotype Deam 6190 US; isotype MO). = Rondeletia deamii (Donn. Sm.) Standley, N. Amer. Fl. 32: 60, 1918.
- 5. "Bouvardia?" discolor Hooker & Arnott, Bot. Beechey Voy. 428, 1840 (Type Andrieux 334 K). = Rondeletia leucophylla H.B.K., fide Standley, N. Amer. Fl. 32: 54, 1918.
- 6. B. ferruginea A. Richard, Mém. Soc. Hist. Nat. Paris 5: 272, 1834, nomen nudum.
- 7. B. havanensis (H.B.K.) A. Richard, loc cit. = Manettia coccinea (Aublet) Willd., fide Standley, N. Amer. Fl. 32: 97, 1921.
- 8. B. hirsuta (Swartz) A. Richard, loc. cit. = Rondeletia hirsuta Swartz, fide Standley, N. Amer. Fl. 32: 75, 1918.
- 9. B. microphylla Schlecht., Linnaea 26: 112, 1854 (Type Schiede s.n. B†), the description is not sufficient for determination.
- 10. B. quinqueflora Dehnhardt, Rivista Napolitana 1, 3: 167. Standley questionably placed B. quinqueflora in the synonymy of B. chrysantha. However, I have been unable to trace Dehnhardt's original publication or the specimen(s) on which it

was based. A description of B. quinqueflora by Walpers (Repert. 2: 507, 1843) is not sufficiently detailed to permit certainty of disposition.

11. B. racemosa (Ruiz & Pavon) A. Richard, Mém. Soc. Hist. Nat. Paris 5: 272, 1834. = ? Mannetia racemosa Ruiz & Pavon.

12. B. scandens A. Richard, loc. cit., nomen nudum.

13. B. strigillosa Baxter, Loudon's Hort. Brit. Suppl. 3: 502, 1850, the description is too scanty for determination.

14. B. strigosa Bentham, Pl. Hartw. 75, 1841 (Type Hartweg 503 K). = Rondeletia strigosa (Bentham) Hemsley, fide Standley, N. Amer. Fl. 32: 50, 1918.

15. B. uniflora (H.B.K.) A. Richard, Mém. Soc. Hist. Nat. Paris 5: 272, 1834. = Manettia coccinea (Aublet) Willd., fide Standley, N. Amer, Fl. 32: 97, 1921.

16. B. viperalis Schlecht., Linnaea 26: 114, 1854 (Type Schiede s.n. B†), the description does not suffice for determination.

17. Cestrum spermacocifolium Willd. ex Roemer & Schultes in L., Syst. Veg. 4: 808, 1819 (Type Humboldt & Bonpland s.n., not seen), provisionally excluded from the synonymy of Bouvardia multiflora. Standley incorrectly says that Willdenow's name was published in synonymy.

18. Hedyotis mexicana Standley, N. Amer. Fl. 32: 104, 1921, as synonym of Bouvardia ternifolia; possibly an error for Hedyotis fruticosa Sessé & Mociño ex DC. (=

Bouvardia obovata H.B.K.).

19. Houstonia ochroleuca Raf., Ann. Gen. Sci. Phys. 5: 226, 1820, based on H. coccinea var. alba Dum. which I have been unable to trace. Merrill (Index Rafinesquianus 226, 1949) states that Houstonia "ochroleuca" Raf. = Bouvardia triphylla Salisb. = B. coccinea (Andrews) Link. The basis of this synonymy is not known.

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New taxa are in **boldface** type, all other taxa are in roman type; numbers in **boldface** type refer to descriptions, numbers in roman type refer to synonyms, numbers with dagger (†) refer to names incidentally mentioned.

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Rubioideae 2†